

VEGETATION HISTORY OF THE PACIFIC COAST STATES AND THE "CENTRAL" SIGNIFICANCE OF THE KLAMATH REGION¹

R. H. WHITTAKER

INTRODUCTION

Among the major developments in the biogeography of the eastern United States were three interrelated ideas: (1) the close floristic relation between the eastern United States and eastern Asia (Gray 1846, 1873, Li 1952), (2) the central relation of the southern Appalachians to eastern vegetation (Adams 1902), and (3) the significance of the mixed mesophytic forests in eastern forest history (Braun 1947, 1950). It is through vegetation history that these points take on their meanings in relation to one another. During the Tertiary, in Oligocene and Miocene time, Arcto-Tertiary forests occupied much of the present temperate latitudes of Eurasia and North America. Although these forests differed from one area to another, there was floristic exchange between the two continents across the Bering land bridge, and the forests showed general floristic similarity around the Northern Hemisphere. With the increasingly dry climates and glaciation of later time, these forests were increasingly fragmented, restricted, and modified, while other, more dry-adapted types of vegetation spread through the interiors of Eurasia and North America. Remnants of the Arcto-Tertiary forests exist now on opposite sides of the two continents—in the eastern United States and eastern Asia, and (with fewer surviving genera) in the western United States and western Europe. In the southern Appalachians especially, mixed mesophytic forests occur which are suggestive of the Arcto-Tertiary forests, have a "central" relation to the forest floras of other parts of the eastern United States, and have strong floristic affinities with forests of eastern Asia.

It is natural to seek a comparable center for western forests. An extensive area of old and geologically complex mountains, the Klamath Ranges, extends from the southern end of the Cascade Range and the northern end of the Great Valley of California, west to the Pacific Ocean. One may observe of these mountains that: (1) The area has, like the Southern Appalachians, one of the most highly complex vegetation patterns in North America (Whittaker 1956, 1960). Into this area extend and meet in a complexly interdigitating pattern, various types of vegetation which form the prevailing climaxes of other areas. All western plant formations dominated by trees occur in the Klamath Region, as in no other area. (2) Those forest formations which are of most highly mixed tree-stratum composition and are thought most to resemble Arcto-Tertiary forests in

¹ A contribution from the Department of Zoology, Washington State University, and the Department of Biology, Brooklyn College. The author's studies in the Klamath Mountains were supported in part by the funds for medical and biological research of the State of Washington Initiative Measure No. 171. The author is indebted to R. W. Chaney, D. I. Axelrod, and H. D. MacGinitie for comments on the manuscript.

the West, occur in this region—the redwood forests and mixed evergreen forests. Of these the mixed evergreen forest is the link between two major fractions of western forest vegetation—the coniferous forests, and the sclerophyll and oak-pine woodland grouping. (3) The Klamath Region has also an exceedingly rich flora for its latitude; it is a center of floristic diversity and narrow endemism (Jepson 1923–25, 1935, Mason 1927, Peck 1941, Detling 1948b), and many plant genera have maximum numbers of species in the West, including endemics, occurring there. One may, with certain qualifications to be observed, regard the Klamath Region as a “center” for the western forests.

The prevailing climax at low elevations over much of the Klamath Region is the Mixed Evergreen Forest (Munz & Keck 1949, 1950, 1959, cf. Cooper 1922, Clark 1937)—mixed forests with two-level canopies of larger evergreen-needleleaf or coniferous trees (*Pseudotsuga menziesii*, *Pinus lambertiana*, *Chamaecyparis lawsoniana*, etc.) and smaller evergreen-broadleaf or sclerophyllous trees (*Lithocarpus densiflora*, *Arbutus menziesii*, *Castanopsis chrysophylla*, *Quercus chrysolepis*, *Umbellularia californica*, etc.), with deciduous trees (*Acer macrophyllum* and *A. circinatum*, *Cornus nuttallii*, *Corylus californica*, *Quercus kelloggii*, etc.), usually present also. In relation to moisture the canopy changes, from mesic stands in which the coniferous stratum is dense and deciduous trees may outnumber sclerophylls, through stands in which the conifers are scattered in open growth above a dense sclerophyll stratum, to more xeric stands in which both strata are open and pines (*P. lambertiana*, *P. ponderosa*) rather than *Pseudotsuga* are principal conifers.

The complex vegetation of the Klamath Region may be conceived in terms of these mixed evergreen forests as the central, prevailing climax or vegetational matrix for the region, giving way to other types of communities in various ways (Whittaker 1960). (1) Within the main area of the mixed evergreen forests, distinctive communities of different composition and structure occur on serpentine and other special parent materials. (2) Toward more humid environments nearer the Coast the density of the conifers increases while that of the sclerophylls decreases, and the mixed evergreen forests gradate into *Pseudotsuga* forests. These in turn gradate into coastal *Sequoia* forests in which sclerophylls are represented by small numbers of stems. (3) Toward the north and higher elevations the sclerophylls decline, and the mixed evergreen forests gradate into montane forests dominated by *Pseudotsuga*, *Abies concolor*, and *Pinus ponderosa*. Toward still higher elevations these gradate into subalpine forests dominated by *Abies procera*, *Tsuga mertensiana*, and (locally) *Pinus monticola* and *Picea breweriana*. (4) Toward the drier interior, *Pseudotsuga* declines and the sclerophyll strata become more open, and the mixed evergreen forests gradate into northern oak woodland (*Quercus kelloggii*, *Q. garryana*) in Oregon, pine-oak foothill woodland (*Pinus sabiniana*, *Quercus douglasii*, *Q. agrifolia*, etc.) in California. (5) Toward the south, the mixed evergreen forests narrow toward the coast (to become part of

the "redwood border" vegetation of the California Coast Ranges), and in drier climates gradate into broad-sclerophyll forests and these into chaparral.

It will be the object of this paper to consider the vegetation history of the Pacific Coast states with special reference to the Klamath Region and two questions—the origin of this vegetation pattern and the central relation of this region to the western forests.

VEGETATION HISTORY

Some aspects of vegetation history bearing on the Klamath Region have been summarized by Chaney (1936, 1938a, 1938c, 1940, 1947, 1948a) and Axelrod (1940a, 1950c, 1952, 1958, 1959). Geological history bearing on the story has been summarized by Diller (1894, 1902), Hershey (1903), Smith & Packard (1919), Clark (1921), Willis (1925), Fenneman (1931), Smith (1933), Reed (1933), Weaver (1937), and Williams (1948).

Pre-Cenozoic (Jurassic and Cretaceous) floras of the Klamath Region and Oregon Coast Ranges are described by Fontaine (1905a, 1905b, 1905c) and Chaney (1948a). Forest trees of more modern types became widespread in Cretaceous time; Cretaceous floras include almost all the families of the subtropical Eocene floras of the West, as represented by the Goshen flora (Chaney & Sanborn 1933). Much of the area of California and Oregon, inland to the Sierra Nevada and Blue Mountains, was submerged in the Cretaceous; the Klamath Region itself formed an extensive, mountainous island which later was probably reduced by erosion and subsidence to an archipelago of scattered islands (Diller 1894, Condon 1902, 1910, Smith & Packard 1919, Smith 1933, Reed 1933). Toward the close of the Cretaceous the Klamath Region was raised above the sea again.

In Eocene time the full land surface of the Klamath Region was occupied by vegetation as it has been (except for local alpine glaciation) through the whole of Cenozoic time since. With continued evolution of modern plant types, extinction of archaic ones, and probable climatic warming accompanied by migrations toward the north, subtropical forests of essentially modern types appeared in the United States in the Eocene, as the Wilcox and other floras of the East (Berry 1916, 1930, 1937), the Goshen and other floras of the West (Chaney & Sanborn 1933, Chaney 1936, 1938c, 1947). During the Eocene epoch, the Oregon coast north from the Klamath Mountains was submerged (Weaver 1937), as was the Great Valley and much of California west of the Sierra Nevada (Clark 1921, Reed 1933). The Oregon and California Coast Ranges were not yet formed, although submarine volcanic activity on an immense scale was producing the lavas later to become the core of the Coast Ranges of Oregon and Washington (Williams 1948). The Cascade Mountains were not yet elevated to intercept the moisture of maritime air masses. Most of Oregon was a broad plain, across which mesophytic forests ex-

tended from the coast to the John Day Basin area of eastern Oregon (Clarno flora, Knowlton 1902, Chaney 1938c, 1948a) and beyond. The high temperatures of the Eocene permitted subtropical floras to extend northward to about 50° north latitude on the coast (Chaney 1947), and some elements of these forests to extend as far as 56–57° in Alaska (Hollick 1936, Chaney 1949).

Mesophytic subtropical forests, representing the Neotropical-Tertiary Geoflora, appear in fossil floras from widely separated points in the Pacific Coast states—from the California Sierra Nevada (Chalk Bluff and La Porte floras, MacGinitie 1941, Potbury 1935), through western Oregon (Comstock and Goshen floras, Sanborn 1935, Chaney & Sanborn 1933, Chaney 1936, 1948a) to the Puget floras of Washington (Newberry 1898, Chaney 1947). Physiognomically, such forests were dominated by trees with leaves of subtropical types—of moderate size, thick and probably evergreen texture, mostly entire margins, and in many cases elongate tips; floristically the Lauraceae (*Cinnamomum*, *Persea*, *Ocotea*, *Neolitsea*, *Cryptocarya*, *Lindera*, *Nectandra*) predominated along with *Ficus*, *Anona*, *Meliosma*, *Magnolia*, and other subtropical or tropical forms. Such subtropical forests doubtless prevailed in the lowlands of the Klamath Region. There is little indication of the upland forests of that time; but it may be presumed that temperate forests, probably including such genera as *Sequoia*, *Pseudotsuga*, and *Abies*, *Alnus*, *Lithocarpus*, and *Ulmus* occurred there (Chaney 1936, 1938a, 1938c) and were related to the temperate forests which then existed far to the north in Alaska (Hollick 1936, Chaney 1938a, 1947).

Much of western California, Oregon, and Washington was submerged during the Oligocene, but the submergence was less extensive in the lands adjacent to the Klamath Region (Clark 1921, Reed 1933, Weaver 1937). Volcanic activity in the area of the Cascade Mountains, which had begun in the Eocene, continued in the Oligocene to form a belt of scattered mountains which were still not effective as a climatic barrier (Williams 1948). In the Klamath Region itself a major uplift believed to have occurred at the close of the Eocene (Diller 1902) initiated the long cycle of erosion which was to produce the Klamath peneplain. With lower temperatures in the Oligocene, subtropical forests were displaced to the south, while the temperate forests were shifted southward and downward. In the western states *Metasequoia* and other temperate forms which had occurred in Alaska entered lowland forests along with *Sequoia* and other forms which had occurred on the uplands of the West during the Eocene (Chaney 1936, 1947, 1951). Through a wide area of the West there occurred forests which may be broadly characterized as redwood-mixed, dominated by either evergreen or deciduous redwood (*Sequoia* or *Metasequoia*, see Chaney 1948b, 1951) mixed with a variety of deciduous and some evergreen broad-leaved trees. These temperate forests of the Eocene in the Far North and the Oligocene and Miocene in the United States, taken in the broad sense and with allowance for the regional and topo-

graphic differentiation within them, represent the Arcto-Tertiary Geoflora (Chaney 1947, 1959). The transition between the Arcto-Tertiary and subtropical forests of the West was apparently represented in moist lowlands by warm-temperate forests in which *Taxodium* was dominant rather than the redwoods, with *Nyssa* as a major broad-leaved form among a mixture of subtropical and temperate forms—forests suggestive of the swamp forests in warm-temperate eastern North America of the present.

Lowland forests of this sort, dominated by *Taxodium* and *Nyssa* and including forms of both temperate (*Metasequoia*, *Juglans*, *Salix*, *Quercus*, *Platanus*, *Tilia*, *Ulmus*) and tropical (*Ocotea*, *Lindera*, *Persea*, *Ficus*) affinities are represented in the Klamath Region by the Oligocene Weaver-ville flora (MacGinitie 1937). Although these do not represent the up-land forests, they imply the prevalence of temperate forests over most of the land surface of the Klamath Region from that time on. Far east from this, the Florissant flora (MacGinitie 1953) occurred in the area of the Colorado Front Range; this flora also included forms of subtropical affinities but was predominantly temperate in character. *Sequoia*, *Chamaecyparis*, *Fagopsis*, and *Zelkova* are believed to have occurred along streams and on moist bottom-lands, broadleaf forests with many forms now represented in forest-grassland transitions of the eastern and south-western states in sites of intermediate moisture conditions, and pine woodland with evergreen oak and chaparral forms on drier uplands. Species of *Picea*, *Abies*, and *Acer* in the flora are believed to represent mountain forests of higher elevations. As observed by MacGinitie (1953, p. 52), the low-elevation pattern from mesophytic streamside forest to pine-oak woodland is suggestive of vegetation patterns now existing in parts of the Klamath Region. A related complex pattern ranging from mesic forest with *Zelkova*, *Cercidiphyllum*, and *Fagopsis* through prevailing deciduous forest to dry-slope communities with pines, sclerophyll oaks and xeric shrubs, with coniferous mountain forests also represented, is described by Becker (1956) from the Ruby River Basin of Montana.

Temperate forests of the upper Oligocene are represented in the Bridge Creek flora of the John Day and Crooked River basins (Knowlton 1902, Chaney 1924, 1925a, 1927, 1938c), forests of redwoods (*Metasequoia*) mixed with many other species, the living relatives of which occur in the West (*Tsuga*, *Abies*, *Taxus*, *Lithocarpus*, *Quercus*, *Acer*, *Alnus*, *Cornus*, *Fraxinus*, *Philadelphus*, *Rhamnus*), and in forests of eastern North America and eastern Asia (*Carpinus*, *Castanea*, *Fagus*, *Liquidambar*, *Nyssa*, *Ostrya*, *Platanus*, *Tilia*, *Ulmus*, *Cercidiphyllum*). Forests of this type, but with *Sequoia* rather than *Metasequoia*, are represented in the Klamath Mountains by the Ashland flora (Chaney 1938c). Although no Oligocene fossils of upland forests are available for the Klamath Region, the Ashland, Florissant, and Bridge Creek floras together suggest a probable vegetation pattern: mesophytic forests of mixed needle-leaved evergreen (*Sequoia*, *Chamaecyparis*, etc.), broad-leaved evergreen (*Quercus*, *Litho-*

carpus, etc.), and deciduous trees, giving way toward higher elevations to cool-temperate forests including *Abies* and *Picea*. In the coastal climate the pattern would be more strongly mesophytic, with less contrast of the extremes of the moisture gradient, than the Florissant pattern. Allowing for a warmer and more humid climate than at present, and the extinction of some early-Cenozoic forms, especially among deciduous trees, this pattern would be not unlike that now occurring in the more humid Klamath Mountains near the coast.

With continued cooling of climates from Oligocene through and beyond Miocene time, the Neotropical-Tertiary flora almost wholly disappeared from most of the United States, though certain members of predominantly tropical and subtropical families became adapted to life in temperate forests and remain as remnants of the Eocene forests (Chaney 1944b, 1947). In the earlier Miocene, the belt of Oregon now occupied by the Coast Range, and additional lands to the west of it, were above sea level (Weaver 1937). Warm-temperate forests including forms of subtropical affinities extended north on this coastal plain through and beyond the Klamath Region, in a manner comparable to that of the vegetation of the coastal plain of the eastern United States today. In floras from Rujada and Cascadia, in west-central Oregon (Chaney 1938c, 1948a), forms of the redwood forests (*Sequoia*, *Lithocarpus*, *Alnus*, *Berberis*) and deciduous trees now extinct in the West (*Tilia*, *Castanea*, *Ulmus*, *Carya*) occur together with subtropical *Persea*, *Ocotea*, and *Sabalites*. In the Klamath Region itself, the long-continued Klamath erosion cycle (Diller 1902) reduced much of the land to a peneplain of gentle or moderate relief. Scattered, low mountain ranges, which later became the monadnock summits of the major mountain groups of the region, rose locally 1000 meters or more above the peneplain. It may be presumed that inland from the coastal plain the Klamath lowlands continued to be occupied by redwood-mixed forests, while mountain forests occurred at higher elevations.

Through later Miocene time, the widespread Arcto-Tertiary forests were affected by increasingly dry climates. Great lava flows successively destroyed existing vegetation in the interior of Oregon and Washington in Miocene and later time (Williams 1948), and formed land surfaces which were occupied by new and more dry-adapted vegetation. In the Mascall flora of the John Day Basin, and related floras widely distributed from California to Washington and Oregon (Knowlton 1902, Chaney 1925b, 1948a, 1959), mixed forests with *Taxodium* and redwoods appeared. The reduction of the redwoods and other mesophytic forms in these suggests, however, a climate drier than that of the Bridge Creek flora (Knowlton 1902, Chaney 1925b, 1938c, 1948a, Axelrod 1940a). Resemblance of these forests to the redwood-border forests was emphasized in earlier accounts (Chaney 1925b, 1938c, Oliver 1934). The redwood in question was the deciduous *Metasequoia*, however; and the oaks were predominantly species with larger, dissected leaves resembling many of those now in the deciduous forests of the eastern states, *Q. kelloggii* and

other deciduous western oaks (Knowlton 1902). The Mascall flora of the John Day Basin was thus a predominantly deciduous forest adapted to still relatively humid, but increasingly continental climates, of eastern Oregon (Chaney 1948a). Forms of subtropical affinities in the Mascall flora and the Latah flora of eastern Washington (Chaney 1938c, 1938a, Knowlton 1926) suggest continued warmth of climate. Mixed forests including conifers (*Sequoia*, *Abies*, *Libocedrus*, *Pseudotsuga*, *Picea*, *Thuja*), sclerophylls (*Lithocarpus*, *Quercus*), and deciduous trees occurred at Weiser, southwestern Idaho (Dorf 1936). A vegetation pattern including mixed sclerophyllous and deciduous trees as the prevailing climax, and a montane forest with *Abies*, *Pinus*, *Pseudotsuga*, and *Chamaecyparis*, is suggested by La Motte (1936) for the upper Cedarville flora of northwestern Nevada and northeastern California. Farther south, vegetation more distinctly adapted to drier climates appeared in the sclerophyll forests of the Tehachapi and Mint Canyon floras (Axelrod 1939, 1940b).

Changing climates of the later Miocene were thus reflected in geographic and topographic shrinkage of the mesophytic, Arcto-Tertiary forests. The complement to this process was the spread of dry-adapted vegetation types and floras, many forms of which expanded northward from centers of origin probably in scattered areas of the Southwest where Neotropical-Tertiary plants became adapted to aridity in Cretaceous and Paleocene time (Axelrod 1958), other forms of which probably evolved from species of temperate forests to occupy cooler dry environments as these became increasingly available, some forms of which entered the North American flora from the dry-climate flora of eastern Asia (Babcock & Stebbins 1938). Because of the importance of the spread out of the Southwest, and of the Mexican mountains as a center, Axelrod (1940a, 1950a, 1950c, 1958) has termed the dry-adapted floras of southwestern derivation, an even broader grouping than the Arcto-Tertiary, the Madro-Tertiary Geoflora.

At the end of the Miocene, the whole Cascade belt was upheaved by folding and tilting (Williams 1948), further desiccating the interior of Oregon and Washington. Uplift occurred in the Klamath Region (Diller 1902, Williams 1948), the Olympic Mountains (Weaver 1937) and the Sierra Nevada (Diller 1894, Fenneman 1931), drying the interior farther south; and further, major uplift occurred at the end of the Pliocene. In Pliocene time most of the coastal belt of Oregon was above the sea, but lobes of the sea extended into some areas of California and Washington (Clark 1921, Reed 1933, Weaver 1937). Deformations producing the California and Oregon Coast Ranges occurred at the beginning and end of the Pliocene. Islands off the California coast, the history of which may be traced backward through earlier Cenozoic time (Reed 1933), supported and permitted the differentiation of the California closed-cone pine flora (Mason 1934, Cain 1944). The trend of increasing dryness of climate continued through the Pliocene, though with fluctuations toward more humid climates during part of the epoch. Axelrod (1944c, 1944d, 1948)

suggests climates which were more humid and warmer than at present in the lower, drier and warmer than at present in the middle, and cooler and moister than at present in the upper Pliocene.

Some of the floras of lower Pliocene (or upper Miocene) age are mesophytic and warm-temperate in character. Coastal plain vegetation of warm climate and moist situations is represented in central California (San Pablo or Neroly flora, Condit 1938, Axelrod 1944d), with forests including *Taxodium*, *Nyssa*, *Persea*, and *Magnolia*. The Remington Hill flora of the Sierra Nevada (Condit 1944a) and the Troutdale flora of the Columbia River Gorge (Chaney 1944a) include *Sequoia* and *Chamaecyparis*, together with deciduous and sclerophyllous broad-leaved trees. These are the last samples of forests of Arcto-Tertiary type in which *Sequoia*, *Chamaecyparis*, and other conifers, *Umbellularia* and other sclerophylls, are mixed with a diverse deciduous component including many genera now restricted to the eastern United States or eastern Asia. *Metasequoia* had apparently become extinct by the end of the Miocene (Chaney 1951). At lower elevations in the area of the Remington Hill flora, the Table Mountain flora (Condit 1944b) included more xerophytic woodland and chaparral forms. Eastward from these areas, forests of the interior are represented in floras of west-central Nevada (Axelrod 1956, 1957), and the Alvord Creek flora of southeastern Oregon (Axelrod 1944e). In the Nevada floras Sierra redwoods (*Sequoiadendron*) occurred with other conifers with modern equivalents in the Sierra Nevada and Klamath Region on cooler slopes, and chaparral on exposed slopes, in vegetation patterns dominated by oak woodlands (Axelrod 1956). At Alvord Creek montane forests of *Pseudotsuga*, *Abies* and *Pinus* on more mesic slopes gave way to woodland and chaparral forms on drier slopes. Vegetation patterns most nearly resembling this contact of an interior, montane derivative of the Arcto-Tertiary forest with Madro-Tertiary woodland occur now in the drier, eastern portion of the Klamath Region. The Alvord Creek flora suggests the increasing importance of conifers other than redwoods (*Pseudotsuga*, *Abies*, *Picea*, *Pinus*) which were to dominate the later forests of the interior. These and other lower Pliocene floras represent the latest occurrence over extensive areas of the West of forest types and vegetation patterns similar to those now existing in the Klamath Region and California Coast Ranges.

With increasing dryness of middle Pliocene and later time, the more strictly mesophytic forms of these forests were eliminated from most or all of the western states. Middle Pliocene Mulholland and Petaluma floras of west-central California, and the Oakdale from the central Sierra (Axelrod 1944a, Dorf 1933, Axelrod 1944b, 1944d) represent oak-woodland communities and reflect the expansion of Madro-Tertiary vegetation. The Deschutes and Alturas floras (Chaney 1938b, Axelrod 1944f) of northeastern California and eastern Oregon, with *Populus*, *Salix*, and other riparian forms of semi-arid climates, indicate the elimination of the mesophytic forests from the lowland interior east of the Cascades. Wood-

land, chaparral, grassland, and desert were spreading over much of the area formerly occupied by forest (Axelrod 1948, 1950c, 1958). Cooler and more humid climates of later Pliocene time are indicated by extension into west-central California of more mesophytic forests—the Sonoma, Wildcat, and Santa Clara floras (Dorf 1933, Axelrod 1944c, 1944d), in which *Sequoia* was present or dominant, together with sclerophyllous and deciduous trees.

The cooler and drier climates of the Pliocene, accompanied by and in part produced by rising mountain ranges along the Pacific Coast, effected the replacement of widespread Arcto-Tertiary forests by essentially modern vegetation patterns. The mesophytic redwood-mixed forests shrank from wide occurrence into a limited area of coastal California and southern Oregon. *Sequoia sempervirens* and *Chamaecyparis lawsoniana* have become wholly restricted to this area; the evergreen-broadleaf or sclerophyll component (*Umbellularia*, *Lithocarpus*, *Castanopsis*, *Arbutus*, and *Quercus* spp.) has become largely restricted to this same coastal belt and somewhat less humid climates inland from it. Deciduous components were even more strongly affected by increasingly dry summer climates. *Metasequoia* and many broad-leaved deciduous forms are extinct in the West; those that have survived have done so by restriction to the same areas of humid forests or to mountain forests, by restriction to valleys and the vicinity of water-courses in more arid regions, or by such adaptations to aridity as are indicated by smaller and thicker leaves (Chaney 1944b). As the range of the mesophytic forests decreased, that of the diverse Madro-Tertiary forms increased; and woodlands and other types of the less humid West spread as regional climaxes (Axelrod 1948, 1958). Floristic differentiation separated the vegetation of southern California from that of northern California (Axelrod 1937, 1950b). Floristic differentiation also separated the forests of the North Pacific Coast, and those of the Rocky Mountains and interior ranges, from those of the California coastal belt (Axelrod 1940a, 1948, 1950c, Mason 1947), although forms now of the North Coast and Rocky Mountains lived with the redwood-mixed forests in the California Coast Ranges into middle or upper Pliocene time (Axelrod 1944a, 1944c, 1948), and many of these forms are represented in the Klamath Region and Cascade Mountains today. Climatic and topographic changes combined to convert mesophytic forest patterns, which changed slowly across great distances of the West, into complex and strongly zoned patterns of many plant communities closely juxtaposed along steep climatic gradients of the mountains and valleys of the Pacific Coast states.

It is thought that during the Pliocene epoch the vegetation of the Klamath Mountains took on essentially its present character. Forests related to the present *Sequoia* and mixed evergreen forests have probably existed in this region, with changing distributional relations to elevation and topography, through most of Cenozoic time. But it is probably in middle Pliocene time that the *Sequoia* forests, which had occurred at

Ashland in the eastern Siskiyou Mountains in Oligocene time, became restricted to the coastal belt, while Madro-Tertiary woodland forms entered the Klamath Region from the south. Thus would result the major features of the modern pattern—coastal redwood forests, mixed evergreen forest in the central portion of the region, and oak woodland and other more xeric types toward its eastern limits.

California Pleistocene floras (Chaney & Mason 1930, 1933, Potbury 1932, Mason 1934) represent essentially modern vegetation types. Climates distinctly cooler than those of the present are indicated, however, by the Willow Creek and Carpinteria floras (Chaney & Mason 1930, 1933); forests corresponding to the former now occur 600 km. or more north along the coast from Santa Cruz Island. The extent to which Pleistocene climates were cooled and vegetation displaced south of the ice sheet in the eastern United States has been debated (Braun 1947, 1950, 1955, Potzger & Tharp 1947, Deevey 1949). The combination of fossil forest types well south of their present occurrence with glacial topography in the higher Klamath Mountains (Hershey 1900, Flint 1957) suggests substantial climatic effects accompanying glaciation in this area. Displacement of the northern limit of the *Sequoia* forest southward, and expansion of the montane forests into lower elevations at the expense of the mixed evergreen forests, are likely. Cooler climates would also displace species which had previously occurred farther north, southward into the Klamath Region. In warmer, post-glacial climates, these species could persist in the area by movement upward in the mountains, as well as northward. Detling (1954) has observed that the flora of Saddle Mountain in the Oregon Coast Range includes a number of boreal relicts resulting from this kind of displacement; a number of these have the present southern limits of their distributions at higher elevations in the Klamath Mountains. Other Klamath species have distributions suggesting that they are relicts from glacial time—notably *Chamaecyparis nootkatensis*, the known southern limit of which is represented by three isolated patches at high elevations in the Siskiyou Mountains, two reported by Mason (1941) and one found by the author on Preston Peak.

Retreat of the glaciers was followed by warmer and drier climates until the xerothermic period, about 4000–8000 years ago, which was drier and warmer than the present (Hansen 1947, Flint 1957). Effects of the drier climate were less evident near the coast than in the interior (Hansen 1947); but vegetational displacements the reverse of those during the glacial periods must have occurred in the Klamath area—with movement northward of the *Sequoia* forests and expansion of the mixed evergreen forests and still more xeric types relative to forests of more mesic situations and higher elevations. Expansion of chaparral over an extensive area of California and northward into the Klamath Region probably occurred also during drier climates of Pleistocene time (Axelrod 1937). Relicts of xerothermic vegetation occur on some peaks west of the Cascades in Oregon, in areas now dominated by mesophytic forests (Detling

1953). Comparable relicts, including some of the species listed by Detling, occur in the Klamath Region, especially on serpentine and other special parent materials and on drier mountain slopes in the eastern part of the region.

THE CENTRAL RELATION OF THE KLAMATH REGION

Major points on the origin of the Klamath vegetation pattern are indicated in the preceding account; they may be summarized: (1) The history of the western forests from Miocene time to the present has been one of progressive shrinkage toward the coast and higher elevations, accompanied by progressive differentiation in the different areas of the West. Within the Klamath Region, mixed forests of Arcto-Tertiary derivation were modified by extinction of the greater share of their tree species, especially among deciduous forms, and became restricted to more humid climates near the coast. (2) From the Arcto-Tertiary forests evolved also, with even more severe depletion of tree species, montane and subalpine forests adapted to environments which were cooler, or drier, or both than those in which the redwood and mixed evergreen forests occur. Higher elevations of the Klamath Region are occupied by montane and subalpine forests which are in large part similar in derivation and character to those of other western mountains, in part distinctive in occurrence of species (*Picea breweriana*, *Quercus sadleriana*, *Ribes marshalli*, etc.) endemic to the Klamath Region. (3) An extensive transition of communities belonging neither simply to Arcto- nor Madro-Tertiary floras has probably existed at least since early Tertiary time and has, with the evolution and differentiation of its own species and evolution of Arcto- and Madro-Tertiary species into and through it, differentiated into various communities occurring between forests and more xeric non-forest communities. The mixed evergreen forests and woodlands of the Klamath Region have probably such mixed derivation from Arcto- and Madro-Tertiary and intermediate floras. Among these communities there is a range of climatic variations and probable derivation, from more mesic types of mixed evergreen forests which are primarily of Arcto-Tertiary derivation, to more xeric pine-oak woodlands primarily of Madro-Tertiary derivation. (4) In reciprocal relation to the forest history, dry-adapted communities progressively expanded and differentiated in the Southwest and interior lowlands, communities predominantly of Madro-Tertiary derivation in the south but with increasing representation of forms of Arcto-Tertiary or other cooler-climate derivation toward the north. As part of this development, woodland, chaparral, and grassland communities spread in the drier inland environments of the Klamath Region.

The thesis has been developed by Braun (1935, 1938, 1947, 1950, p. 39, 1955) that the Mixed Mesophytic Association of the Appalachian Plateaux is the central, the oldest, and the most complex association of the Deciduous Forest Formation, that from the Mixed Mesophytic, or its ancestral progenitor, the mixed Tertiary forest, all other climaxes of the

deciduous forest have arisen. The corresponding relation of the coastal redwood and mixed evergreen forests of the Klamath Region to the western forests is suggested, but a number of qualifications on too literal an interpretation of this relation should be observed. The Arcto-Tertiary forests were not "a community," but a vegetation pattern with marked regional differentiation in dominance and floristic composition, with differentiation also in relation to moisture gradients and presumably other local factors. Their species were variously distributed, and widespread species probably showed marked ecotypic differentiation then, as today (Axelrod 1941). Much of the West has been occupied by vegetation at all times; and the effect of climatic change was not to segregate different forest types from a single ancestral type, but to cause increasing local differentiation of forests that were already regionally differentiated in the Oligocene and Miocene. Many tree species and species-groups have been in existence through the whole of the Cenozoic (Stebbins 1950); and many of the trees of the West have some history of association with redwoods and the Arcto-Tertiary forests (Mason 1947). But the species and ecotypic populations that have evolved into the present have been variously associated with one another and total community floras variously derived from different sources, resulting from diverse patterns of evolution and migration in different species and species-complexes. In evolutionary time species change their patterns of ecotypic differentiation and association with other species; and the evolution of communities is reticulate, not simply divaricate (Mason 1936, 1947, Whittaker 1957). If the forests of the West are in part derived by differentiation from the redwood-mixed forests, they may also be derived in part from other coniferous forest communities whose history in the West—in higher elevations and drier situations in the mountains—may go back as far as that of the redwood-mixed forests. Resemblance of the coastal redwood and mixed evergreen forests to the earlier redwood-mixed forests does not imply that the former are in any very real sense ancestral to western forests in general. It implies only that, in the progressive shrinkage, species-extinction, and regional differentiation of the western forests from the Miocene to the present, the largest fraction of Arcto-Tertiary forms, representing all three tree growth-forms, survived in the most favorable climate—that of the Klamath Region and northern California Coast Ranges.

One reason for the "central" relation of the Klamath Region thus lies in geographic and climatic circumstance. It is in this region, as in the Southern Appalachians in the East, that a combination of sufficient humidity and warmth of climate occurs to support mesophytic, mixed forests which are most like Arcto-Tertiary forests among existing vegetation types. Location and climate of the Klamath Region, and the steep climatic gradient from the coast inland, are responsible also for much of the vegetational diversity of the region, and for the meeting there of plant communities of diverse climatic and geographic relations.

The notable floristic diversity of the region is also in part a conse-

quence of edaphic diversity. Geological history has resulted in an unusually complex mosaic of parent materials, often with striking effects on vegetation and flora (Whittaker 1954, 1960). Parent material contrasts also contribute to the meeting of community-types and species of widely different geographic relations. Thus at low elevations in the central Siskiyou Mountains, *Chamaecyparis-Pseudotsuga* forests with deciduous and sclerophyll trees and Northwestern floristic affinities, and Jeffrey pine woodlands with *Libocedrus decurrens* and *Arctostaphylos viscida* and floristic affinities with the montane forests of the Sierra Nevada, occur in close proximity—but the former on diorite, the latter on serpentine. Many of the numerous species which reach their distributional limits in the Klamath Region occur there as localized, “relict” populations on serpentine, gabbro, or other special parent materials. Greatest numbers of narrowly endemic species occur on these same parent materials; other narrow endemics appear on more “normal” parent materials at high elevations and in other special situations. Concentrations of narrowly endemic species in the area are thus related to edaphic factors (cf. Mason 1946a, 1946b) and other environmental extremes (cf. Detling 1948a).

The Klamath Region thus shares characteristics with other centers of floristic diversity and narrow endemism—topographic complexity, edaphic diversity, and age of land surfaces. The diversity of habitats has been characteristic of the area throughout its long history, although climatic gradients were probably less steep before middle Pliocene time. Even at the maximum development of the Klamath peneplain, mountains of diverse parent materials existed in the area. The region has at all times offered a complex mosaic of habitats in which species of diverse environmental requirements might survive, while submergence, glaciation, climatic desiccation, and lava flows have affected surrounding areas. From the unlimited diversity of the present geographic and probable historic relations of species represented in the area, one may recognize such major groupings as: (1) widespread western species, and Sierra-Cascade species, which extend through the region; (2) formerly more widespread species which are now relict endemics or epibiotics in the region; (3) species of diverse present distributional relations which extend, from the south, the north and the interior, into communities in appropriate climates in the region, many of these species being at or near their limits of distribution there; (4) species of diverse distributional relations represented in the region by localized, “relict” populations on special parent materials, at higher elevations, or both; (5) narrowly endemic species of diverse origin, many of which may have evolved within the region to occupy some part of its complex mosaic of habitats.

The central relation of the Klamath Region is regarded primarily not as one of a center of origin for forests of other parts of the West, but as a center toward which mesophytic forests of the past have shrunk, and as a center of accumulation of species of varied evolutionary history in the diverse habitats of ancient land surfaces. This does not mean, however,

that the area has not also been a center of origin of major significance for some groups of plants—a reservoir of species populations of diverse environmental adaptations and of genetic diversity within some species and species-complexes, from which populations have evolved and migrated into other areas. The genus *Crepis* provides an example (Babcock & Stebbins 1938), with a number of diploid species now relict in the Klamath area, while genetic material from these has been used in apomictic polyploids which have spread over semi-arid environments of the interior. The cytogenetics of *Crepis* further suggest that endemic species shared by the Klamath Region and the Tehaman area of the northern Sierra Nevada (Jepson 1923–25) have reached the latter from the Klamath Mountains (Babcock and Stebbins 1938).

It may be noted that the two aspects of the central relation of the Klamath Region discussed are to some extent separate phenomena. The central vegetational relation is a consequence of location and climate, primarily because of adjacency to the Coast; the concentration of species diversity and endemism is a consequence of climatic and edaphic diversity and age, primarily because of the mountains inland from the coastal belt. A series of criteria for centers were suggested by Adams (1902, 1909); but these are each subject to limitations and are to some extent independent of one another (Cain 1944). “Centers” are conceptual products of interpretation according to chosen criteria (Whittaker 1956). The Klamath Region is by no means the only center for forest vegetation and flora in the West. The Sierra Nevada is of comparable antiquity; this and other California ranges are rich in species, including narrow endemics. A center of maximum development of coniferous forests may be located in the Puget Sound area, and the center for the sclerophyll complex is well to the south of the Klamath Region. In the complex vegetational and floristic pattern of the West there may be no single area which has the same degree of “central” significance as the Southern Appalachians in the East. Yet, when these various allowances are made, it remains true that the Klamath Region possesses a central relation to other forest areas which is one of the significant features of the biogeography of the western United States.

SUMMARY

1. The Klamath Region of northwestern California and southwestern Oregon is an area of old and geologically complex mountains, supporting a complex vegetation pattern and a diverse flora rich in narrowly endemic species. The region is a floristic and vegetational “center” for the forests of the western United States.

2. Vegetation history of the Pacific Coast states since Miocene time has involved progressive shrinkage of Arcto-Tertiary forests and progressive expansion and differentiation of Madro-Tertiary communities. Mixed forests (coastal *Sequoia* and mixed evergreen forests) most nearly related to the Arcto-Tertiary forests in the West are now limited to the Klamath

Region and northern California Coast Ranges, while woodland, chaparral, and grassland communities primarily of Madro-Tertiary derivation have entered the Klamath Region from the south to form the more xeric part of its vegetation pattern.

3. Floristic diversity of the Klamath Region has resulted from climatic and parent-material diversity, together with age of the mountains which has permitted species of diverse histories and environmental relations to survive there, often as relicts restricted to special parent materials or situations.

Biology Department, Brooklyn College
Brooklyn 10, New York

LITERATURE CITED

- ADAMS, C. C. 1902. Southeastern United States as a center of geographical distribution of fauna and flora. *Biol. Bull.* 3:115-131.
- . 1909. The Coleoptera of Isle Royale, Lake Superior, and their relation to the North American centers of dispersal. *An Ecological Survey of Isle Royale, Lake Superior. Mich. Geol. Rept.* 1908:157-215.
- AXELROD, D. I. 1937. A Pliocene flora from the Mount Eden beds, southern California. *Publ. Carnegie Inst. Wash.* 476:125-183.
- . 1939. A Miocene flora from the western border of the Mohave Desert. *Publ. Carnegie Inst. Wash.* 516:1-129.
- . 1940a. Late Tertiary floras of the Great Basin and border areas. *Bull. Torrey Club* 67:477-487.
- . 1940b. Mint Canyon flora of southern California: A preliminary statement. *Am. Jour. Sci.* 238:577-585.
- . 1941. The concept of ecospecies in Tertiary paleobotany. *Proc. Natl. Acad. Sci. Wash.* 27:545-551.
- . 1944a. Pliocene floras of California and Oregon. 5. The Mulholland flora. *Publ. Carnegie Inst. Wash.* 553:103-146.
- . 1944b. Pliocene floras of California and Oregon. 6. The Oakdale flora. *Publ. Carnegie Inst. Wash.* 553:147-165.
- . 1944c. Pliocene floras of California and Oregon. 7. The Sonoma flora. *Publ. Carnegie Inst. Wash.* 553:167-206.
- . 1944d. Pliocene floras of California and Oregon. 8. The Pliocene sequence in central California. *Publ. Carnegie Inst. Wash.* 553:207-224.
- . 1944e. Pliocene floras of California and Oregon. 9. The Alvord Creek flora. *Publ. Carnegie Inst. Wash.* 553:225-262.
- . 1944f. Pliocene floras of California and Oregon. 10. The Alturas flora. *Publ. Carnegie Inst. Wash.* 553:263-284.
- . 1948. Climate and evolution in western North America during Middle Pliocene time. *Evolution* 2:127-144.
- . 1950a. Studies in late Tertiary paleobotany. I. Classification of the Madro-Tertiary Flora. *Publ. Carnegie Inst. Wash.* 590:1-22.
- . 1950b. Studies in late Tertiary paleobotany. III. Further studies of the Mount Eden flora, southern California. *Publ. Carnegie Inst. Wash.* 590:73-117.
- . 1950c. Studies in late Tertiary paleobotany. VI. Evolution of desert vegetation in western North America. *Publ. Carnegie Inst. Wash.* 590:215-306.
- . 1952. A theory of angiosperm evolution. *Evolution* 6:29-60.
- . 1956. Mio-Pliocene floras from west-central Nevada. *Univ. Calif. Publ. Geol. Sci.* 33:1-322.
- . 1957. Late Tertiary floras and the Sierra Nevada uplift. *Bull. Geol. Soc. Am.* 68:19-45.
- . 1958. Evolution of the Madro-Tertiary Geoflora. *Bot. Rev.* 24:433-509.

- . 1959. Geological history. In *A California flora*, by P. A. Munz & D. D. Keck, pp. 5-9. Univ. Calif. Press, Berkeley & Los Angeles.
- BABCOCK, E. B. AND G. L. STEBBINS, JR. 1938. The American species of *Crepis*; their interrelationships and distribution as affected by polyploidy and apomixis. Publ. Carnegie Inst. Wash. 504:1-199.
- BECKER, H. F. 1956. An Oligocene flora from the Ruby River Basin in southwestern Montana. Ph.D. thesis, Univ. Mich., Ann Arbor. 208 pp.
- BERRY, E. W. 1916. The Lower Eocene floras of southeastern North America. Prof. Paper U. S. Geol. Surv. 91:1-481.
- . 1930. Revision of the Lower Eocene Wilcox flora of the southeastern states, with descriptions of new species, chiefly from Tennessee and Kentucky. Prof. Paper U. S. Geol. Surv. 156:1-196.
- . 1937. Tertiary floras of eastern North America. Bot. Rev. 3:31-46.
- BRAUN, E. LUCY. 1935. The undifferentiated deciduous forest climax and the association-segregate. Ecology 16:514-519.
- . 1938. Deciduous forest climaxes. Ecology 19:515-522.
- . 1947. Development of the deciduous forests of eastern North America. Ecol. Monogr. 17:211-219.
- . 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia. 596 pp.
- . 1955. The phytogeography of unglaciated eastern United States and its interpretation. Bot. Rev. 21:297-375.
- CAIN, S. A. 1944. Foundations of plant geography. Harper, New York & London. 556 pp.
- CHANEY, R. W. 1924. Quantitative studies of the Bridge Creek flora. Am. Jour. Sci., ser. 5, 8:127-144.
- . 1925a. A comparative study of the Bridge Creek flora and the modern redwood forest. Publ. Carnegie Inst. Wash. 349:1-22.
- . 1925b. The Mascall flora—its distribution and climatic relation. Publ. Carnegie Inst. Wash. 349:23-48.
- . 1927. Geology and palaeontology of the Crooked River Basin, with special reference to the Bridge Creek flora. Publ. Carnegie Inst. Wash. 346:45-138.
- . 1936. The succession and distribution of Cenozoic floras around the northern Pacific Basin. In *Essays in geobotany in honor of William Albert Setchell*, ed. T. H. Goodspeed, pp. 55-85. Univ. Calif. Press, Berkeley.
- . 1938a. Paleoeological interpretations of Cenozoic plants in western North America. Bot. Rev. 4:371-396.
- . 1938b. The Deschutes flora of eastern Oregon. Publ. Carnegie Inst. Wash. 476:185-216.
- . 1938c. Ancient forests of Oregon; a study of earth history in western America. Publ. Carnegie Inst. Wash. 501:631-648.
- . 1940. Tertiary forests and continental history. Bull. Geol. Soc. Am. 51:469-488.
- . 1944a. Pliocene floras of California and Oregon. 12. The Troutdale flora. Publ. Carnegie Inst. Wash. 553:323-351.
- . 1944b. Pliocene floras of California and Oregon. 13. Summary and conclusions. Publ. Carnegie Inst. Wash. 553:353-373.
- . 1947. Tertiary centers and migration routes. Ecol. Monogr. 17:139-148.
- . 1948a. The ancient forests of Oregon. Oregon State System of Higher Education (Condon Lectures), Eugene. 56 pp.
- . 1948b. The bearing of the living *Metasequoia* on problems of Tertiary paleobotany. Proc. Natl. Acad. Sci. Wash. 34:503-515.
- . 1949. Early Tertiary ecotones in western North America. Proc. Natl. Acad. Sci. Wash. 35:356-359.
- . 1951. A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. Trans. Am. Philos. Soc., N.S. 40(3):171-239.

- . 1959. Miocene floras of the Columbia Plateau. I. Composition and interpretation. Publ. Carnegie Inst. Wash. 617:1-134.
- CHANEY, R. W. and H. L. MASON. 1930. A Pleistocene flora from Santa Cruz Island, California. Publ. Carnegie Inst. Wash. 415:1-24.
- . 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. Publ. Carnegie Inst. Wash. 415:45-79.
- CHANEY, R. W. and ETHEL I. SANBORN. 1933. The Goshen flora of west-central Oregon. Publ. Carnegie Inst. Wash. 439:1-103.
- CLARK, B. L. 1921. The marine Tertiary of the West Coast of the United States; its sequence, paleogeography, and the problems of correlation. Jour. Geol. 29: 583-614.
- CLARK, H. W. 1937. Association types in the north coast ranges of California. Ecology 18:214-230.
- CONDIT, C. 1938. The San Pablo flora of west-central California. Publ. Carnegie Inst. Wash. 476:217-268.
- . 1944a. Pliocene floras of California and Oregon. 2. The Remington Hill flora. Publ. Carnegie Inst. Wash. 553:21-55.
- . 1944b. Pliocene floras of California and Oregon. 3. The Table Mountain flora. Publ. Carnegie Inst. Wash. 553:57-90.
- CONDON, T. 1902. The two islands. Rev. ed., 1910, Oregon geology: A revision of "The Two Islands," ed. by Ellen C. McCornack. J. C. Gill, Portland, Ore. 187 pp.
- COOPER, W. S. 1922. The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities. Publ. Carnegie Inst. Wash. 319:1-124.
- DEEVEY, E. S., JR. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Am. 60: 1315-1416.
- DETLING, L. E. 1948a. Environmental extremes and endemism. Madroño 9:137-149.
- . 1948b. Concentration of environmental extremes as the basis for vegetation areas. Madroño 9:169-185.
- . 1953. Relict islands of xeric flora west of the Cascade Mountains in Oregon. Madroño 12:39-47.
- . 1954. Significant features of the flora of Saddle Mountain, Clatsop County, Oregon. Northw. Sci. 28:52-60.
- DILLER, J. S. 1894. Tertiary revolution in the topography of the Pacific Coast. U. S. Geol. Surv., 14th Ann. Rept., 1892-93 (Part II):397-434.
- . 1902. Topographic development of the Klamath Mountains. Bull. U. S. Geol. Surv. 196:1-69.
- DORF, E. 1933. Pliocene floras of California. Publ. Carnegie Inst. Wash. 412:1-112.
- . 1936. A late Tertiary flora from southwestern Idaho. Publ. Carnegie Inst. Wash. 476:73-124.
- FENNEMAN, N. M. 1931. Physiography of western United States. McGraw-Hill, New York. 534 pp.
- FLINT, R. F. 1957. Glacial and Pleistocene geology. Wiley, New York. 553 pp.
- FONTAINE, W. M. 1905a. The Jurassic flora of Douglas County, Oregon. *In* Status of the Mesozoic floras of the United States, second paper, ed. L. F. Ward. Monogr. U. S. Geol. Surv. 48:48-145.
- . 1905b. Plants from Curry County, Oregon. *In* Status of the Mesozoic floras of the United States, second paper, ed. L. F. Ward. Monogr. U. S. Geol. Surv. 48:148-151.
- . 1905c. Notes on some fossil plants from the Shasta group of California and Oregon. *In* Status of the Mesozoic floras of the United States, second paper, ed. L. F. Ward. Monogr. U. S. Geol. Surv. 48:221-277.
- GRAY, A. 1846. Analogy between the flora of Japan and that of the United States. Am. Jour. Sci. & Arts 52:135-136.
- . 1873. Address of Professor Asa Gray, ex-president of the Association. Proc. Am. Assoc. Adv. Sci. 21:1-31.

- HANSEN, H. P. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. *Trans. Am. Philos. Soc.*, N.S. 37(1):1-130.
- HERSHEY, O. H. 1900. Ancient alpine glaciers of the Sierra Costa Mountains in California. *Jour. Geol.* 8:42-57.
- . 1903. Structure of the southern portion of the Klamath Mountains, California. *Am. Geol.* 31:232-245.
- HOLLICK, A. 1936. The Tertiary floras of Alaska, with a chapter on the geology of the Tertiary deposits by P. S. Smith. *Prof. Paper U. S. Geol. Surv.* 182:1-185.
- JEPSON, W. L. 1923-25. A manual of the flowering plants of California. Univ. Calif. Assoc. Students Store, Berkeley. 1238 pp.
- . 1935. Centers of plant endemism in California in relation to geological history. *Proc. Zesde Internatl. Bot. Congr., Amsterdam* 2:82-83.
- KNOWLTON, F. H. 1902. Fossil flora of the John Day Basin, Oregon. *Bull. U. S. Geol. Surv.* 204:1-153.
- . 1926. Flora of the Latah formation of Spokane, Washington, and Coeur d'Alene, Idaho. *Prof. Paper U. S. Geol. Surv.* 140:17-81.
- LAMOTTE, R. S. 1936. The upper Cedarville flora of northwestern Nevada and adjacent California. *Publ. Carnegie Inst. Wash.* 455:57-142.
- LI, HUI-LIN. 1952. Floristic relationships between eastern Asia and eastern North America. *Trans. Am. Philos. Soc.*, N.S., 42(2):371-429.
- MACGINITIE, H. D. 1937. The flora of the Weaverville beds of Trinity County, California, with descriptions of the plant-bearing beds. *Publ. Carnegie Inst. Wash.* 465:83-151.
- . 1941. A Middle Eocene flora from the central Sierra Nevada. *Publ. Carnegie Inst. Wash.* 534:1-167.
- . 1953. Fossil plants of the Florissant beds, Colorado. *Publ. Carnegie Inst. Wash.* 599:1-198.
- MASON, H. L. 1927. Fossil records of some West American conifers. *Publ. Carnegie Inst. Wash.* 346:139-158.
- . 1934. Pleistocene flora of the Tomales formation. *Publ. Carnegie Inst. Wash.* 415:81-179.
- . 1936. The principles of geographic distribution as applied to floral analysis. *Madroño* 3:181-190.
- . 1941. The Alaska cedar in California. *Madroño* 6:90.
- . 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño* 8:209-226.
- . 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. *Madroño* 8:241-257.
- . 1947. Evolution of certain floristic associations in western North America. *Ecol. Monogr.* 17:201-210.
- MUNZ, P. A. and D. D. KECK. 1949. California plant communities. *El Aliso* 2:87-105.
- . 1950. California plant communities—supplement. *El Aliso* 2:199-202.
- . 1959. A California flora. Univ. Calif. Press, Berkeley & Los Angeles. 1681 pp.
- NEWBERRY, J. S. 1898. Later extinct floras of North America. Ed. posthumously by A. Hollick. *Monogr. U. S. Geol. Surv.* 35:1-295.
- OLIVER, ELIZABETH. 1934. A Miocene flora from the Blue Mountains, Oregon. *Publ. Carnegie Inst. Wash.* 455:1-27.
- PECK, M. E. 1941. A manual of the higher plants of Oregon. Binford & Mort, Portland. 866 pp.
- POTBURY, SUSAN S. 1932. A Pleistocene flora from San Bruno, San Mateo County, California. *Publ. Carnegie Inst. Wash.* 415:25-44.
- . 1935. The La Porte flora of Plumas County, California. *Publ. Carnegie Inst. Wash.* 465:29-81.
- POTZGER, J. E. and B. C. THARP. 1947. Pollen profile from a Texas bog. *Ecology* 28:274-280.

- REED, R. D. 1933. *Geology of California*. Am. Assoc. Petroleum Geol., Tulsa, Oklahoma, and Murby, London. 355 pp.
- SANBORN, ETHEL I. 1935. The Comstock flora of west-central Oregon. Publ. Carnegie Inst. Wash. 465:1-28.
- SMITH, W. D. 1933. Geology of the Oregon coast line. *Pan.-Am. Geol.* 59:33-44, 97-114, 190-206, 241-258.
- SMITH, W. D. and E. L. PACKARD. 1919. The salient features of the geology of Oregon. *Jour. Geol.* 27:79-120.
- STEBBINS, G. L., JR. 1950. *Variation and evolution in plants*. Columbia Univ. Press, New York. 643 pp.
- WEAVER, C. E. 1937. Tertiary stratigraphy of western Washington and northwestern Oregon. *Univ. Wash. Publ. Geol.* 4:1-266.
- WHITTAKER, R. H. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. *Ecology* 35:275-288.
- . 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26:1-80.
- . 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. *Am. Jour. Bot.* 44:197-206, & *In Fifty years of botany; golden jubilee volume of the Botanical Society of America*, ed. W. C. Steere, 1958, pp. 344-358. McGraw-Hill, New York.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30:279-338.
- WILLIAMS, H. 1948. The ancient volcanoes of Oregon. Oregon State System of Higher Education (Condon Lectures), Eugene. 64 pp.
- WILLIS, R. 1925. Physiography of the California Coast Ranges. *Bull. Geol. Soc. Am.* 36:641-678.

GERMINATION OF CEANOTHUS SEEDS¹

CLARENCE R. QUICK AND ALICE S. QUICK

The many species of ceanothus in California are ecologically diverse, but they occur most frequently and most abundantly on relatively arid sites and where repeated wildfire has been a determinant of vegetative composition. Because of prompt and abundant seedling regeneration after fire (Quick, 1959) and because many or all ceanothus species have nitrogen-fixing nodules on their roots (Quick, 1944), the genus is an important factor in development and conservation of high-quality soil profiles under wildland vegetation. In order to survive fire, seeds "stored" in duff and topsoil must lie in relatively well-insulated positions and be quite obdurate to heat (Quick, 1956).

Most ceanothus seeds will not imbibe water and "plump" in the laboratory unless they are first subjected to some type of heat treatment (Quick, 1935), or to seed-coat scarification. Unplumped seeds cannot germinate because they are dry. Seeds of montane species of ceanothus commonly will not germinate, even if thoroughly plumped, unless an embryo dormancy has been obviated by appropriate stratification treatment; i.e., by continuously-moist aerated storage for some weeks at temperatures slightly above freezing. The present paper reports data from experiments aimed

¹Facilities for seed storage and culture, stratification and germination were made available by the California Forest and Range Experiment Station, United States Forest Service, in cooperation with the University of California at Berkeley.